

ZOOPLANKTON FEEDING ECOLOGY: CONTENTS OF FECAL PELLETS OF THE COPEPOD *CENTROPAGES VELIFICATUS* FROM WATERS NEAR THE MOUTH OF THE MISSISSIPPI RIVER

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ABSTRACT

The *in situ* diet of the copepod *Centropages velificatus* was investigated using scanning electron microscopy. Contents of fecal pellets produced upon natural diets were compared with assemblages of available phytoplankton. Samples came from continental shelf waters near the mouth of the Mississippi River. A wide variety of particle sizes and types were ingested. The dominant phytoplankton taxa in pellets sometimes mirrored those dominant in the water, particularly if these were large solitary cells or elongate chains of smaller cells. However, in other cases the dominant phytoplankton remains in pellets were those of cells that were not abundant in the water. Crustacean remains and fine particles of silt from the river plume were also frequent dominant components. *C. velificatus* is clearly an omnivore.

The often poor correspondence between ingested and abundant phytoplankton taxa and the frequency of crustacean remains suggests that this copepod spends much of its time feeding as a raptorial carnivore upon other zooplankton.

INTRODUCTION

Omnivorous feeding is common in planktonic marine copepods. Numerous species ingest both phytoplankton and zooplankton (reviewed by Turner, 1984a), and some large copepods can eat larval fish (Turner *et al.*, 1985 and references therein). However, most studies of copepod omnivory have used laboratory diets such as cultured phytoplankton and zooplankton. Examinations of the diets of omnivorous copepods feeding upon natural food assemblages have been less frequent.

As part of a study of planktonic food webs that support larval fish in northern Gulf of Mexico continental shelf waters, an effort has been made to define diets of copepod species that are prey of fish larvae (Turner, 1984b, c, d, 1985, 1986a, 1986b). Contents of fecal pellets produced from food ingested prior to capture have been compared with co-occurring phytoplankton species assemblages. A general pattern that has emerged for many calanoid species is that of indiscriminant suspension feeding; phytoplankton taxa in fecal pellets reflect the composition of the natural phytoplankton. However, certain copepods such as the large calanoid *Labidocera aestiva* (Turner, 1984c) or several cyclopoid species (Turner, 1986b) did not exhibit this pattern as strongly as other typically herbivorous species. The fecal pellets of *L. aestiva* and the cyclopoids contained considerable crustacean remains, and disproportionately high abundances of large phytoplankton cells that were not particularly abundant in the water. These results suggest that these copepods are primarily raptorial omnivores, feeding frequently on other animals and large phytoplankton cells.

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In addition to the largely qualitative fecal pellet studies, we have performed quantitative grazing studies on three species of calanoid copepods: *Acartia tonsa*, *Eucalanus pileatus*, and *Centropages velificatus* (Turner and Tester, 1986; Tester and Turner, 1986). Although *A. tonsa* and *E. pileatus* exhibited nonselective grazing, with phytoplankton taxa being ingested in proportion to their abundance, this pattern did not hold for *C. velificatus*. Regression coefficients between rates of ingestion of individual phytoplankton taxa and abundance of those taxa, or between total phytoplankton ingestion rate and total phytoplankton abundance were low. This suggested that *C. velificatus* was feeding primarily as a carnivore, a detritivore, or as a selective herbivore upon less-abundant phytoplankton. Accordingly, the contents of *C. velificatus* fecal pellets produced at these and other northern Gulf of Mexico stations were examined with the scanning electron microscope (SEM).

Centropages velificatus Oliveira is widely distributed throughout the tropical and subtropical western Atlantic and Gulf of Mexico (Fleminger and Hulsemann, 1973). This species is the Atlantic cognate of the Indo-Pacific species *Centropages furcatus* Dana (Fleminger and Hulsemann, 1973). Thus, numerous Atlantic and Gulf of Mexico records for *C. furcatus* (Owre and Foyo, 1967 and references therein; Bowman, 1971; Paffenhöfer and Knowles, 1980) apply to *C. velificatus*. This copepod is one of the numerically dominant mesozooplanktonic calanoids in continental shelf waters of the northern Gulf of Mexico (Marum, 1979; Minello, 1980), and it is consumed in these waters by several species of fish larvae (Govoni *et al.*, 1983).

Various *Centropages* species have long been known to be omnivores, ingesting both cultured phytoplankton, *Artemia* nauplii, or cultured copepod nauplii (reviewed by Turner, 1984a). Paffenhöfer and Knowles (1980) found that *C. velificatus* from the southeastern United States continental shelf ingested a higher percentage of its body nitrogen in the form of laboratory-reared copepod nauplii (*Pseudodiaptomus coronatus*) than as large diatoms of the genus *Rhizosolenia*. However, the temperate congener *C. hamatus* ingested a higher percentage of its body carbon as natural phytoplankton than as field-caught copepod nauplii (mostly *Acartia* spp.) (Conley and Turner, 1985). In addition, *C. typicus* has been shown to ingest yolk-sac larvae of two fish species (Turner *et al.*, 1985).

Results presented here support previous *Centropages* feeding studies, as well as the suggestion from our quantitative grazing data (Turner and Tester, 1986; Tester and Turner, 1986) that *C. velificatus* is a raptorial omnivore, feeding to a great extent upon large phytoplankton cells and other crustaceans. This is, to my knowledge, the first study of the *in situ* feeding habits of this copepod.

MATERIALS AND METHODS

Samples were collected from ten stations (Table I) on three cruises in 1982 and 1983. Surface water samples (500 ml) for phytoplankton analyses were preserved in Utermöhl's solution (Guillard, 1973) immediately prior to zooplankton tows. Surface tows with 363 μm mesh nets were used for copepod collection. The mesh was coarse enough to allow passage of all phytoplankton and microzooplankton, thereby preventing possible net feeding. Copepods were immediately sorted by pipette and isolated in surface seawater within 5–15 min of collection. After pellets reflecting gut contents upon capture had been produced (usually < 0.5 h), they were individually removed by pipette, placed in a mixture of filtered seawater and 20 μm -mesh-screened surface water (containing natural microbes), and left for 24–36 h at approximately 20°C for microbial stripping of pellet peritrophic membranes, which if left intact, mask contents (Turner, 1978; 1979). Pellets were preserved in 5% formalin: seawater solutions for analyses ashore.

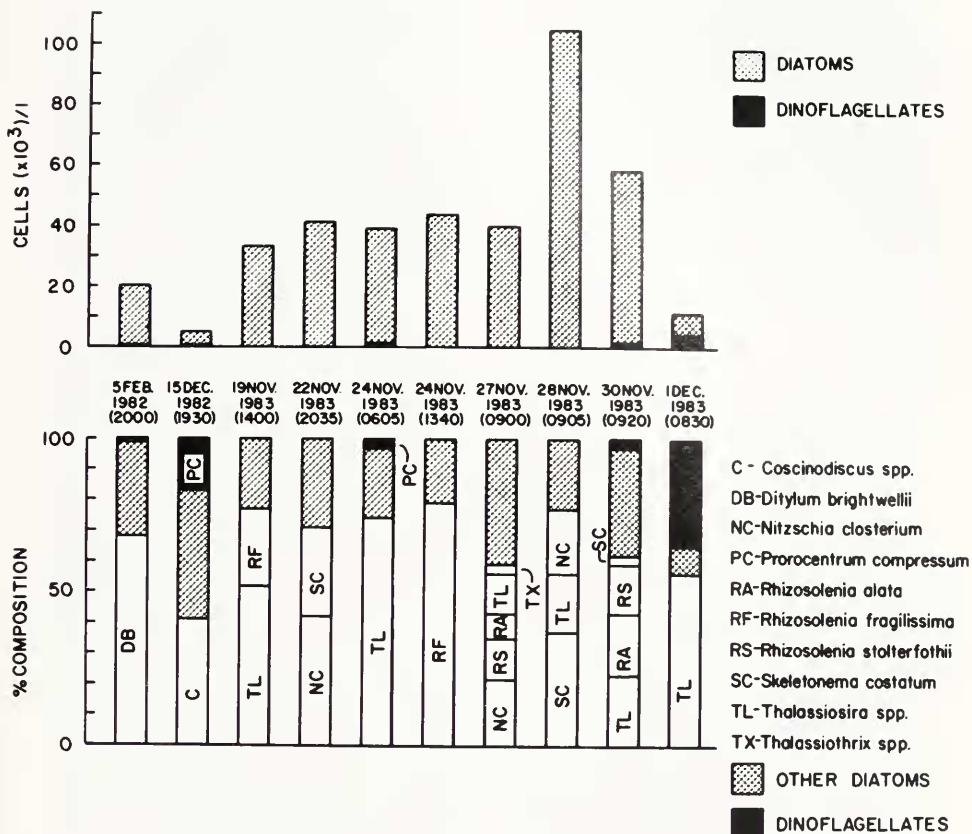


FIGURE 1. Abundance (upper) and composition (lower) of natural phytoplankton assemblages in surface waters at sampling stations.

Preserved pellets were individually sorted by pipette and drawn onto Whatman* GFC glass fiber filters. Filters with attached pellets were washed in distilled water for salt elimination, dehydrated in a graded ethanol series, critical point dried, coated with gold;palladium, and examined with a ISI-30 SEM at 15 kV.

All fecal pellets were from *Centropages velificatus* adult females. One hundred twenty-two (122) micrographs were taken from 38 fecal pellets. SEM examination preceded phytoplankton analyses to avoid possible bias in characterization of pellet contents. Entire visible sides of each pellet were examined. The 26 micrographs presented here (21% of those taken) are representative of pellet contents. Phytoplankton analyses were made with the Utermohl inverted microscope technique (Lund *et al.*, 1958).

RESULTS

Abundance and species composition of surface phytoplankton varied considerably (Fig. 1). Abundance ranged from 5.4–105.1 $\times 10^3$ cells/l. With the exception of

* Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE I

Locations, times, and surface salinities of sampling stations

Date	Local time	Latitude (N)	Longitude (W)	Surface salinity (‰)
5 Feb. 1982	2000	28°53'	89°29'	21.5*
15 Dec. 1982	1930	28°54'	89°28'	18.1*
19 Nov. 1983	1400	28°52'	89°29'	—*
22 Nov. 1983	2035	28°50'	98°30'	31.5
24 Nov. 1983	0605	28°53'	89°29'	31.8
24 Nov. 1983	1340	28°51'	89°25'	29.6*
27 Nov. 1983	0900	29°02'	89°30'	26.1
28 Nov. 1983	0905	28°48'	89°57'	26.6
30 Nov. 1983	0920	28°48'	89°58'	30.7
1 Dec. 1983	0830	28°52'	89°29'	21.0*

* Stations with a high silt load.

two stations, assemblages were dominated by diatoms. However, on 15 December 1982, the dinoflagellate *Prorocentrum compressum* comprised 17% of total cells, and on 1 December 1983 a combination of the dinoflagellates *P. compressum*, *P. micans*, and *Gyrodinium* sp. comprised 35% of cells present. Abundant diatoms included large solitary cells such as *Ditylum brightwellii* (16.5 x 148.5 µm), *Coscinodiscus* sp. (33–53 µm diameter), and *Thalassiosira* sp. (13–36 µm diameter). Also abundant were various chain-forming diatoms such as *Rhizosolenia fragilissima*, *R. stouterfothii*, and *Skeletonema costatum*.

In addition to phytoplankton, silt from the plume of the Mississippi River was abundant in surface waters from half of the stations (Table I).

Contents of fecal pellets varied widely among stations. At three stations from the river plume (5 February 1982, 19 November 1983, and 24 November 1983 at 1340 h) silt was the only component of fecal pellets (Figs. 2a, b, c), despite the presence of abundant phytoplankton (Fig. 1). Water samples from the station on 15 December 1982 also contained a heavy silt load, but fecal pellets contained primarily cells of the large (33 µm diameter) dinoflagellate *Prorocentrum compressum* (Fig. 2d) in addition to silt. It is interesting that at this station *P. compressum* comprised only 11% of cells counted, whereas the similarly large (33–53 µm diameter) diatom *Coscinodiscus radiatus* comprised 41% of cells counted, but no *C. radiatus* remains were observed in pellets. At other stations, however, large solitary centrics of the genus *Thalassiosira* (26–33 µm diameter) were present in pellets as either intact cells or cell fragments (Figs. 2e, f, 3a, b, c, d). *Thalassiosira* abundance at these stations was high, with values of 35.7, 23.4, and 6.5×10^3 cells/l on 24 November, 28 November, and 1 December 1983, respectively, accounting for 74%, 19%, and 56% of cells on these dates. In addition to *Thalassiosira* spp., pellets from 24 November 1983 (0605 h) contained fragments of *P. compressum* cells (Fig. 3e) and remains of crustaceans (Fig. 3f). Crustacean remains, probably of copepod nauplii, were present in pellets from all remaining stations (Fig. 4c, d, 5d, 6f), along with remains of both small and large diatoms (Figs. 4a, b, 5a, b, 6a, b, c, d) and dinoflagellates (Figs. 5c, 6e). These three stations (22 November, 27 November, 30 November 1983) all had intermediate levels of phytoplankton abundance (Fig. 1), intermediate to high salinity, and reduced silt load (Table I). It is interesting that phytoplankton taxa of long linear dimension such as solitary *Thalassiothrix* sp. cells (up to 154 µm long) or chains of *Skeletonema costatum* (maximum chain length unknown) were the most common phytoplankton

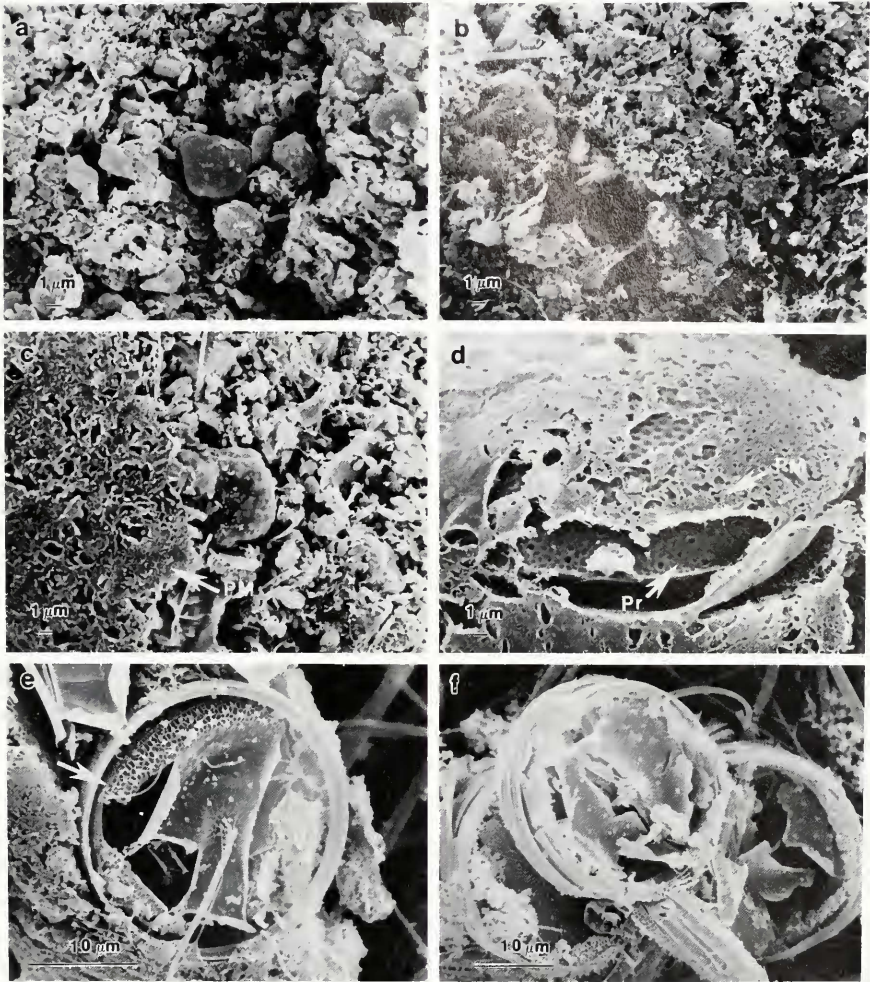


FIGURE 2. Contents of *Centropages velificatus* fecal pellets. a, 24 November 1983 (1340), b, 19 November 1983, c, 5 February 1982 (note peritrophic membrane, PM), d, 15 December 1982 (note peritrophic membrane, PM, and *Procerentrum compressum* cell, Pr), e, 1 December 1983 (note *Thalassiosira* sp. cell at arrow), f, 28 November 1983 (note *Thalassiosira* sp. cells).

observed in pellets from 27 and 30 November (Figs. 5a, b, 6a, b), even though these taxa comprised only 3% each, respectively, of the cells in these samples. Small solitary diatom cells, though sporadically present in pellets (Fig. 4a, b, 6c), were never a dominant component.

DISCUSSION

Centropages velificatus is clearly an omnivore. Fecal pellets representing *in situ* feeding contained primarily the remains of other crustaceans and large or elongate phytoplankton taxa. These field results support previous laboratory studies with the same species (Paffenhöfer and Knowles, 1980) or laboratory and field studies with

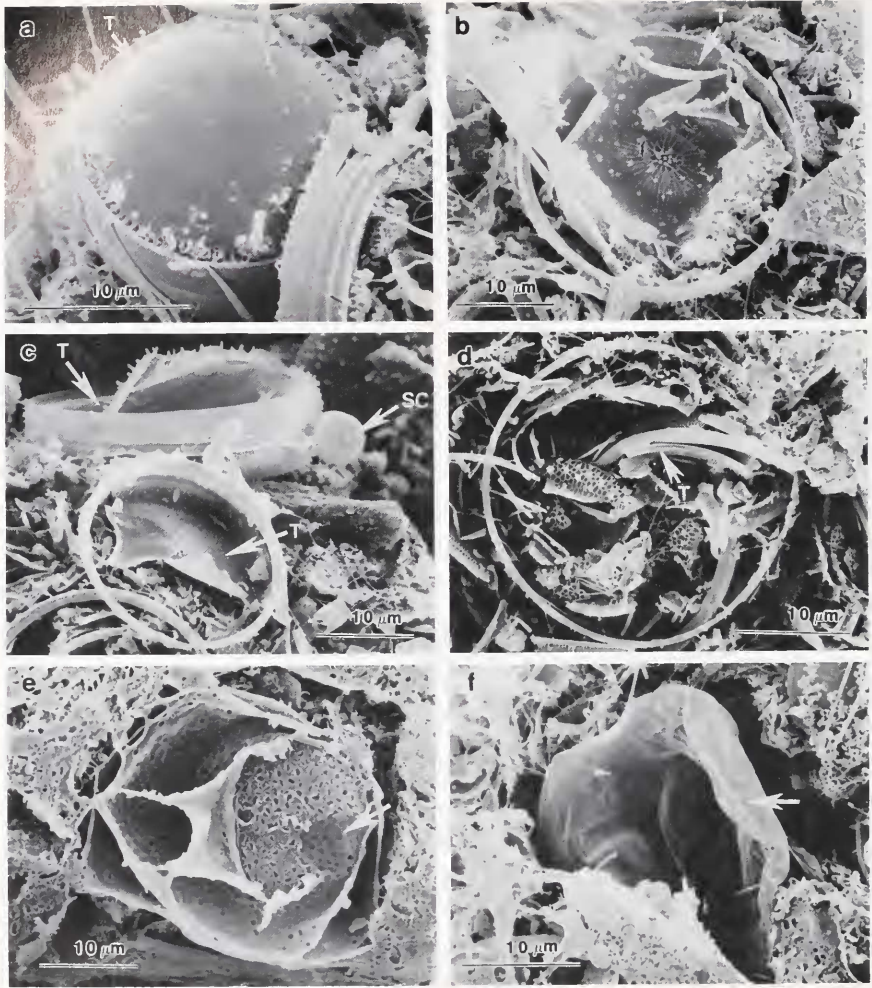


FIGURE 3. Contents of *Centropages velificatus* fecal pellets from the station on 24 November 1983 (0605). a. and b. *Thalassiosira* sp. cells (T). c. *Thalassiosira* sp. (T) and small centric (SC) diatom cells. d. *Thalassiosira* sp. fragments (T). e. *Prorocentrum compressum* cell (arrow). f. crustacean fragment (arrow).

congeners (Turner 1984a and references therein; Conley and Turner, 1985; Turner *et al.*, 1985).

The apparently frequent use of carnivory by *C. velificatus* is also suggested by quantitative grazing data from the northern Gulf of Mexico (Turner and Tester, 1986; Tester and Turner, 1986). Regression coefficients for grazing *versus* available phytoplankton gave poor correlation. Such uncoupling of grazing effort and phytoplankton abundance would be expected if *C. velificatus* feeds primarily as a carnivore, or selectively upon less-abundant phytoplankters.

Although the presence of primarily large phytoplankton cells in fecal pellets is suggestive of selective grazing on large particles, such a conclusion is not without ambiguities. For reasons detailed in Turner (1984c, p. 279) and (1984 d, p. 82), it is impossible to realistically make SEM analyses of fecal pellets quantitative. Further, it is not clear why *Prorocentrum compressum* cells were common in pellets but un-

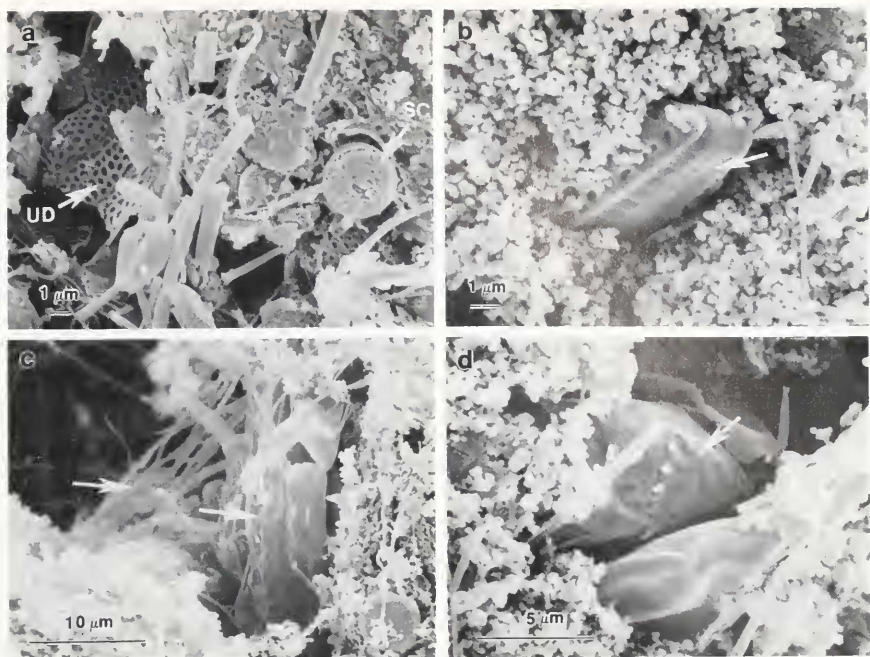


FIGURE 4. Contents of *Centropages velificatus* fecal pellets from the station on 22 November 1983. a. Fragments of an unidentified diatom (UD) and a small centric (SC) diatom. b. pennate diatom (arrow). c. and d. crustacean fragments (arrows).

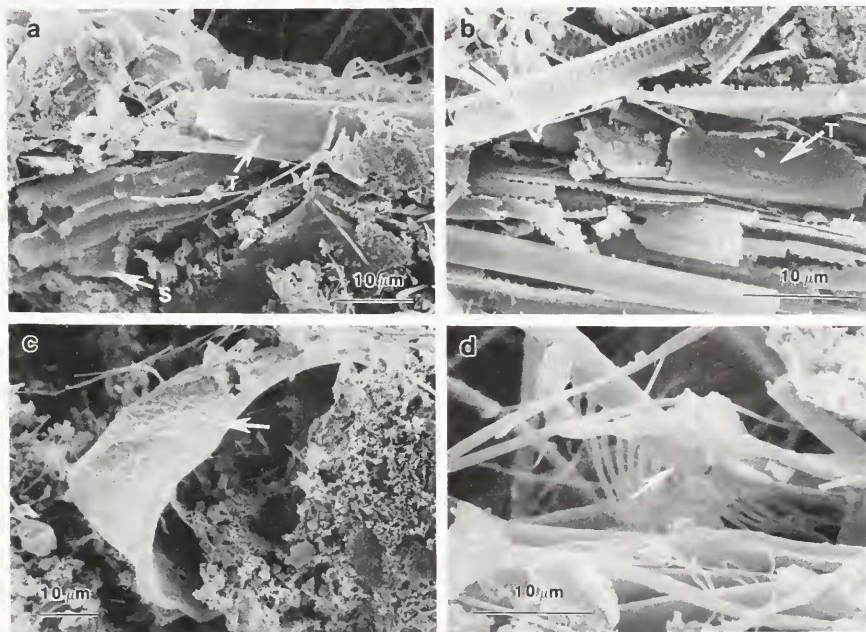


FIGURE 5. Contents of *Centropages velificatus* fecal pellets from the station on 27 November 1983. a. and b. *Thalassiothrix* sp. (T) and *Skeletonema costatum* (S) fragments, c. unidentified dinoflagellate fragment (arrow), d. crustacean remains (arrow).

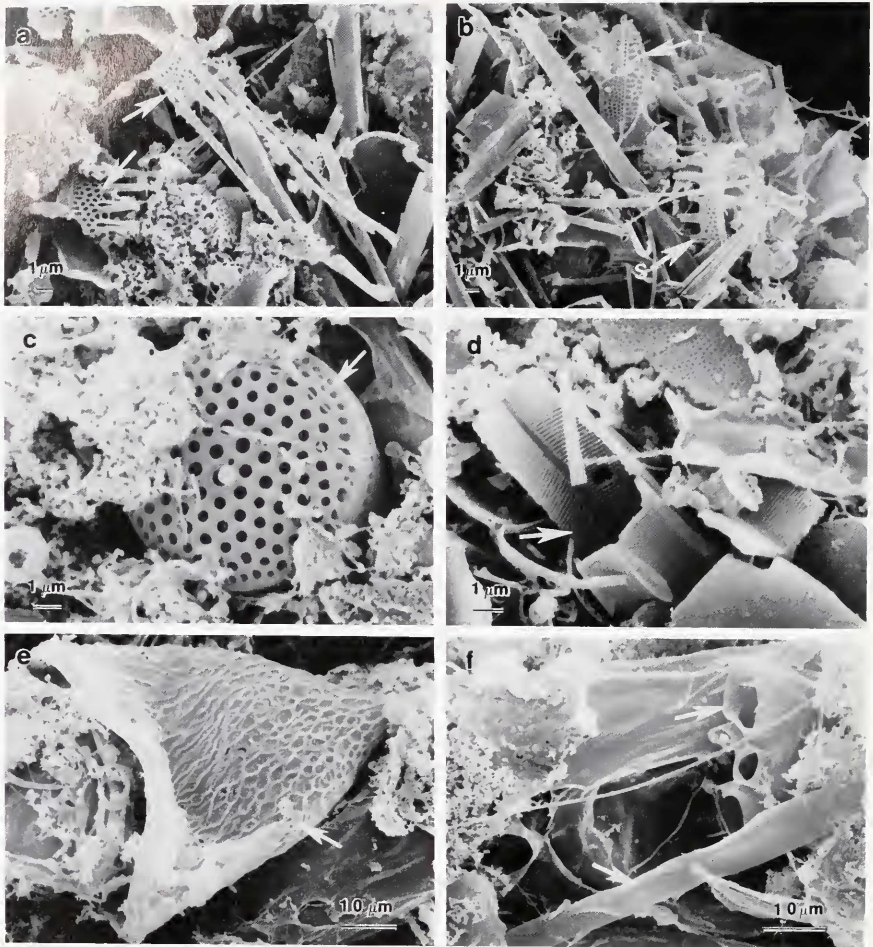


FIGURE 6. Contents of *Centropages velificatus* fecal pellets from the station on 30 November 1983. a. *Skeletonema costatum* fragments (arrows), b. *Skeletonema costatum* (S) and *Thalassiosira* sp. (T) fragments, c. intact centric diatom cell (arrow), d. *Thalassiothrix* sp. fragments (arrow), e. fragment of an unidentified dinoflagellate (arrow), f. crustacean remains (arrows).

common in the water (11% of total cells) on 15 December 1982, whereas the similarly large (33 μm diameter, or larger) diatom *Coscinodiscus radiatus* was not observed in these pellets even though it comprised 41% of available cells. In other cases, large *Thalassiosira* spp. cells were abundant in pellets, but since they were also abundant in the water, this pattern is more indicative of nonselective than selective feeding. Conversely, the disproportionately high abundances in pellets of elongate cells of *Thalassiothrix* sp. or *Skeletonema costatum* cells from elongate chains, when these taxa comprised only a small proportion of available cells, may indicate size selection on 27 and 30 November 1983. In short, there was no consistent pattern of ingestion of large versus small, solitary versus chain-forming, or diatom versus dinoflagellate cells. The production of fecal pellets containing primarily fine-grained silt particles reveals that small particles can also be ingested in large numbers. *Centropages velificatus* apparently employs a variety of mechanisms to capture food from a broad range

of particle sizes. Such varied feeding mechanisms have been demonstrated with high-speed cinematography for *Centropages typicus* (Cowles and Strickler, 1983) and other copepods (Price *et al.*, 1983).

The raptorial omnivory of *Centropages velificatus* evidenced by fecal pellet contents is atypical of many other copepod species studied with the same techniques. Mainly nonselective suspension feeding characterized *Eucalanus pileatus* (Turner, 1984b; Tester and Turner, 1986), *Paracalanus quasimodo* (Turner, 1984b), *Acartia tonsa* (Turner, 1984c; Tester and Turner, 1986), *Temora turbinata* and *T. stylifera* (Turner, 1984d), *Anomalocera ornata* (Turner, 1985), and *Undinula vulgaris* (Turner, 1986a). However, the frequent feeding of *C. velificatus* upon other crustaceans and larger, often less-abundant phytoplankters is similar to the patterns for *Labidocera aestiva* (Turner, 1984c) and several cyclopoids (Turner, 1986b). These results emphasize that when considering the trophic positions or impacts of "copepods" it is important to specify which ones.

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